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MODELING THE EFFECTS OF POLLUTANTS ON THE PROCESSES OF TREE GROWTH

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ABSTRACT. Policy relevant modeling of the effects of pollutants on tree and forest growth need to achieve two goals. First, they must encapsulate our understanding of the processes by which trees grow and by which pollutants act. Second, they must provide the ability to make plausible projections of the response of trees and forests to alternative pollution scenarios in order to assess the potential effects of regulatory action. Here we present the background considerations and an account of work in progress for a modeling system of tree growth designed to meet these needs. The modeling system consists of a series of related models each of which can be studied alone or in concert as they form a whole tree. These individual models are characterized by consideration of both physiology and morphology. Taken together as a Simple Whole Tree (SWT) model they can account for synergies and compensations at the level of the whole tree as it responds to pollutant effects. This approach allows the relative evaluation of different hypothesized mechanisms of action of pollution.

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INTRODUCTION

We describe scientific issues relevant to modeling the effects of pollutants on tree and forest growth at the mechanistic level and how they can be resolved within the context of a large national research program. We use models as vehicles for achieving an integration of knowledge and for making predictions about likely effects under a range of different pollution scenarios. Results must be synthesized from a variety of experiments and investigations. How effective such a synthesis can be depends, not only on the extent of our understanding of pollutant influence on component tree growth processes, but particularly upon our quantitative understanding of tree growth as an integrated process. As we research pollutant effects we increasingly ask new questions about tree physiology and forest processes and it is these questions that dominate our uncertainty about pollutant influences.

THE PURPOSE AND CHALLENGE OF MODELING TREE RESPONSE TO POLLUTANTS

The National Acid Precipitation Assessment Program (NAPAP, 1988) wish to evaluate the complex of evidence describing the effect of acid precipitation on trees and forests and provide answers to the multiple questions that policy makers ask. These include considerations of different levels of acid precipitation, both more and less than currently measured, changes in the balance of chemical elements contributing to the deposition, and the effects of regional variation in control or mitigation.

The Forest Response Program (FRP) is the component program of NAPAP investigating forests (Schroeder and Kiester, 1989). Much of its work is to survey the potential damage. A parallel program of experimental work and of analysis of forest processes is investigating possible mechanisms by which acid precipitation may effect tree and forest growth. That work is organized to investi-

gate particular theories of potential influence e.g. that acid precipitation causes changes in soil properties that influence root growth or function, that acidic precipitation increases nutrient loss from foliage.

The need for process based models

These requirements, prediction for policy purposes and synthesizing results of very different types of investigation, dictate two features of the modeling activity being developed by the Synthesis and Integration Team of the FRP.

First, the *requirement for prediction beyond current conditions* demands that models simulate mechanisms of interaction between pollutant influence and growth. We cannot *depend* solely upon statistical models produced from the results of field investigations made under current conditions because such investigations do not alow us to predict what may happen under different deposition patterns. Nor can we *depend* solely upon experiments conducted with seedlings and necessarily with restricted sets of treatments; these cannot be relied upon to tell us sufficient about the response of mature trees and forests. We consider the most important requirement is that model structure should be functionally correct in the description of mechanisms of response and particularly for mature trees and forests. Scientifically this is the most demanding aspect of our modeling task. Theories of pollution influence, and of the processes that control the growth of large trees are developing continuously and this has important implications for the way in which we develop and use our models.

Second, models must be constructed to *assess* the relative importance of different mechanisms, singly and in combinations, perhaps with different emphasis in different regions and conditions of pollutant load. Models are quantitative representations of theory and in different geographical regions theories of pollution influence with different emphasis are being developed.

This means that no one single, global model will be adequate for the purpose of the FRP. We can expect to construct and use different models, not just one model with different parameters.

Synergistic effects and compensating mechanisms in the response to pollutants

To extrapolate from experiments under controlled conditions we have to be particularly careful to estimate the effects of synergisms and compensating mechanisms. Synergisms occur where the effect of acidic precipitation on two or more processes has a greater effect than can be estimated from studies of the individual processes themselves. Compensating processes may reduce an impact of damage that may be estimated from experiments on single processes. However, these two mechanisms are not immediately apparent and we must develop theories about them that can be incorporated into a more complete theory of pollution influence. Typically synergisms and compensations operate through mechanisms at higher levels of organization than can usually be inestigated through direct experiment, such as through the organizational structure of the whole tree or the stand.

It is conceivable, for example, that a synergistic effect could occur through the effects of acid precipitation on soil and foliar processes. That taken together a small increase in foliar leaching, and a small increase in soil leaching could, over time, have a marked effect upon growth. For example, Hari *et al.* (1987) proposed a complex sequence for the influence of acid precipitation on Finnish forests where there is first an increased nutrient mobilization in the soil and a concomitant increase in tree growth, but, under sustained acid precipitation, then nutrient leaching reduces nutrient levels in the whole ecosystem, in such a way that there is a rapid and dramatic decrease in growth. To examine a theory of synergistic effects between root-

soil and foliar response we may need to simulate the rates at which nutrient loss from foliage can be compensated for by increased nutrient uptake or mobilization within the tree.

A possible *compensating mechanism* in the response of forest stands to acidic precipitation might involve the interaction between a genetically based differential in the response of individual trees to acidic deposition and the competition process that also results in differential growth rates. A theory could be proposed that while acidic deposition might reduce the growth of some individuals within a stand this would, in effect, mitigate the competition process and so perhaps the reduction in growth for a whole stand would be less than might have been estimated by direct experimentation of the primary effect of acid precipitation. To assess this it would be important to simulate the spatial and temporal characteristics of differential growth rates between trees as due to the two processes, i.e., genetically determined sensitivity to acidic precipitation and competition (Webb and Burkhart, 1988).

Implications for model development, use and structure.

We emphasize that process based models should be treated as developing theory. We suggest they should be modular in construction, that the modules should be documented as components of a theory and that they can be replaced. In particular, because investigation of compensating and synergistic effects seems likely to require the use of models, then we need to pay particular attention to higher order properties of trees and forests than we might expect to investigate experimentally. Consequently we are developing a structure in our simulation approach that pays particular attention to how component physiological processes are connected in time and space.

This leads us to a formulation for models of tree and forest growth that use tree morphology and phenology as concepts for organizing physiological processes. This is a new development in whole tree models that challenges some

of the concepts most frequently used, for example, in the article by Bassow, Ford and Kiester (this volume) two such concepts, *allocation* and *maximum foliage amount*, are examined.

DEVELOPMENT OF A THEORY FOR TREE AND FOREST GROWTH

Our starting point for a theory of individual tree growth is similar to that for indeterminate plant growth described by Thornley (1972) (Fig. 1). He described growth as the result of feedback control between root growth and its function of nutrient uptake and foliage growth and its function of photosynthetic production. He modeled growth as a balance between the rates of nitrogen, (N) uptake and transfer to foliage, and photosynthetic production (C) and transfer to roots. The rates of uptake were determined by the respective sizes of root and foliage and a controlling point in his model was the maintenance of a constant internal soluble C and N concentrations.

Figure 1.

The value of Thornley's approach is that the equations for growth, and particularly the relative growth rates of root and foliage, are fully specified in terms of the growth processes themselves. The model does not require terms for the relative allocation of either photosynthate or N to different plant parts and that can only be obtained through empirical studies of weight increment itself. So, the model can be used as a predictive tool the value of which rests upon the theory that internal concentrations of N and soluble C remain constant as growth takes place, and the accuracy with which it represents the processes of photosynthesis, nutrient uptake, translocation and conversion of N and C into dry weight.

One of the six suggested mechanisms of action of acidic precipitation on tree growth is an influence on allocation (Schroeder and Kiester, 1989). While this may be measured in dose-response experiments with seedlings, accurate, direct measurement for large trees and forests, particularly under different conditions of acid precipitation is a task that is beyond our capabilities and is not being attempted within the FRP. We will be dependent upon model based predictions in our assessments. Clearly Thornley's (1972) approach has great utility for this purpose if it can be modified for application to tree growth. In particular we propose that the following must be considered.

(1) Unlike the indeterminate plants which Thornley (1972) modeled, the onset, cessation, and some aspects of the rate of meristem growth rate in trees are controlled through phenological processes (references).

(2) The structure of the tree may determine the rates of growth processes (discussed below). Tree structure determine rates of transport of water, nutrients and photosynthate between roots and foliage, and also the amounts of those quantities that may be stored and available for the growth process.

(3) We can not assume, as did Thornley (1972), that relative growth of roots and foliage is set by a mechanism within the plant that maintains a balance in internal nutrient and carbohydrate concentration. Ingestad (1982) has proposed a theory, based on experiments with tree seedlings, that growth is a function of internal nutrient concentration, and has shown that such concentrations may change as growth proceeds. Further, we know that substantial storage and re-translocation of both carbohydrate and nutrients occurs within perennials and that we must account for this processes in a model based approach.

The first two propositions require that we introduce concepts of form and timing into our theory. The third recognizes that the experimental evidence for a mechanism that maintains constant internal concentrations does not extend in its simplest form to tree species and that within trees there are substantial patterns of storage and re-distribution of both carbohydrate and nutrients - these too require that we understand the spatial distribution of different tissues.

The mechanism of tree growth

The theory of tree growth that we are using (Fig. 2) is developed from the general theory described by Thornley (1972). This represents a Simple Whole Tree model (SWT) where each compartment has a structure that can be expressed in terms of mass and morphology and which is the result of carbon gain. The *structure* of each compartment influences the processes of carbon, water and nutrient uptake and/or movement and so defines the *functional* properties that determine the amount of further growth that will be made. The interactions between the three compartments are determined by the rates and absolute mass of transfer between them of carbon, water and nutrients.

This is not an appropriate venue for a detailed review of the literature that has been required to formulate propositions for the three compartments. What follows is a summary of work in progress for two aspects of SWT, the distribution of foliage on a branched structure and the translocation of photosynthate. These examples are selected to describe the aspects of SWT that differ from other modeling approaches to whole tree growth.

Figure 2.

The distribution of foliage on a branched structure.

Our starting point is a model (Ford and Ford 1988) for branch growth (Fig. 3) that simulates the following interactions:

i *phenology*, which is determined by a set of hypotheses defining the timing of different growth processes and in which shoot extension plays a major role,

ii *morphology*, which is determined by hypothesized processes defining the numbers of branch segments produced from each bud, their orientation and their absolute and relative lengths,

iii *foliage development and function*, a set of hypotheses defining the production of foliage on branchlets, its rate of production of biomass and how this changes with time, and the rate of foliage mortality, and

iv *branch wood thickening*. Hypotheses are proposed that define the amount of wood increment at different positions along a branch. The first algorithm used has been to calculate branchwood thickening in relation to the structural requirements to maintain a particular curvilinear relationship of branch posture (McMahon and Kronauer 1976).

Figure 3.

Export to the mainstem is the residual production after shoot extension, foliage growth and branch thickening have been satisfied under the various hypotheses. Simulation is at the level of the whole branch, i.e., the carbon balance of individual branch segments are not considered separately.

Two versions of BRANCH exist. One requires a statistical description of the morphological development of the branch that is species specific, BRANCH 1 (Fig. 4). A second requires that the branching at each growing tip of the branch as it develops follows rules specified by the environment of the tip, BRANCH 2 (Fig. 5). The two models are currently being used to explore the structure of the model itself and particularly to investigate various alternative hypotheses for such functions as the control of wood increment along the branch as it grows.

From a simulation with BRANCH 1 the branch drawn in Fig. 4 has a structure similar to that typically found in spruce, referred to as Pattern 1, and is drawn after 8 years of simulated growth. A ratio of the lengths of side branches to apices of 0.7 was used in that simulation, and the outputs from the simulation in terms of annual leading shoot extension, foliage weight on the branch, and material exported to the trunk, are drawn in solid lines. The lower right hand graph depicts the angular distribution of the branch at its death. The branch is assumed to die when it makes no more extension of its main shoot axis and this occurs when all the photosynthate produced is required to maintain the branch structure. When the side branch ratio is reduced to 0.5, and still considering Pattern 1 (dashed line) then, although the extension of the main axis is not reduced, the growth of side branches is as also is the production of foliage and the amount of material exported to the trunk. Simulations using Pattern 2 describe a distinct relationship between the extension length of a segment and the number of branchlets arising from it (>40 cm, 7 branchlets; >30, 5; >20, 3; >10, 1; <10, 0). This turns out to be a more stringent limitation of branchlet production and results in earlier accumulation of foliage weight and export of material to the main trunk. A ratio of side branch to main branch length of 0.7 for Pattern 2 being approximately equivalent in total amounts of these quantities to that of a ratio of 0.5 for Pattern 1.

In Fig. 5 we explore the consequences of varying the numbers of branches in a whorl, using BRANCH 2. This is possible with this model because the interaction between branchlets is simulated as a form of lateral competition. In the figure it can be seen that the greatest return to stem is attained from a branch in a whorl of 4. When the cumulative export to the trunk, over the full life of the branches and for the whole whorl was considered, then a branch number per whorl of 4 was greatest of those shown and also exceeded that for 3 branches per whorl.

Figure 4.

Figure 5.

Simulating the transport of water and photosynthate

Two types of observations suggest that water and carbohydrate transport rates may vary according to the size of the tree. First there is the observation that in older trees the duration of periods of low shoot water potential is extended (Waring, Whitehead and Jarvis, 1979) over that typically found in younger forest trees (e.g. Milne, Ford and Deans, 1983). This may have implications, not only for direct effects of low water potential on such processes as stomatal conductance or cell expansion, but also for nutrient flux to the foliage and carbohydrate flux to the roots. Second, it is apparent that much of the annual root increment in trees may be constructed from stored carbohydrate reserves (e.g. Deans and Ford, 1986). As trees age then pre-growth period starch concentrations in roots appear to decrease. We need to explore the extent to which this may be a response to an increased transport pathway, a decrease in photosynthetic production relative to requirements for growth and respiration, or some other mechanisms.

The basic theory that we are using to model translocation is Münch Pressure Flow (e.g. Tyree *et al.*, 1974 and Smith *et al.*, 1980). In this theory water potential gradients have a controlling influence upon translocation (Fig. 6) and must be modeled directly.

Figure 6.

We are developing a water transport model (HYDRA). To date construction of a process-based model of tree water relations that can predict gradients of water potentials within the tree have been hampered by: 1) lack of inclusion of spatial detail in whole-tree morphology, and 2) lack of ability to predict resistance to water flow from tissue characteristics. We are developing in both of these directions with HYDRA by exploring the implications of wood structure on both macroscopic and microscopic scales. Haskins and Ford (this volume) examine relevant cellular and whole-tree models, and use simulation to explore possible interaction of flow through an individual tracheid and flow through tissues with a variety of tracheid size distributions. An important problem is to achieve a definition of the capacitance of trunks and how this may vary both with wood structure and amount and in relation to actual water potential gradients.

We are developing a non-steady state model of Münch Pressure flow, TRANS. As a first step, phloem sieve tubes are considered to be long tubular columns of sieve cells, separated by sieve plates. The sieve plates act as a resistance to flow down the sieve tube, causing successive pressure drops. Fig. 7 illustrates the sieve tube and the variables incorporated in TRANS (based on Tyree *et al.*, 1974 and Smith *et al.*, 1980). The variables of the model are given in Table 1. The effects of all of the sieve plates are averaged together in the calculation of sieve tube hydraulic conductivity, denoted γ.

Table 1.

Figure 7.

Flow of sucrose solution down the sieve tube, caused by the mechanism of Münch Pressure flow, can then be calculated by the following two partial differential equations for conservation of sucrose and water volume (Smith *et al.*, 1980):

1. Conservation of Water Volume

$$\frac{\partial}{\partial t}[1-\bar{V}C(x,t)]A\Delta x = J_s(x_1)[1-\bar{V}C(x_1)]A + 2\pi r\Delta x J_w(x) - J_s(x_2)[1-\bar{V}C(x_2)]A$$

with the passive water influx defined as:

$$J_w(x) = L_p[\Psi_0(x) - P(x) + C(x)RT]$$

and the velocity or volume flux at x is:

$$J_s(x) = -\gamma\frac{\partial P}{\partial x}(x)$$

The conservation of water equation can be rewritten as:

$$\frac{\partial}{\partial t}[1-\bar{V}C(x,t)] + \frac{\partial}{\partial x}\left[-\gamma\frac{\partial P}{\partial x}(1-\bar{V}C(x,t))\right] = \frac{2L_p}{r}[\Psi_0(x,t) - P(x,t) + C(x,t)RT]$$

2. Conservation of Sucrose

$$\frac{\partial C}{\partial t}(x,t)A\Delta x = q(x)\Delta x + AJ_s(x_1)C(x_1) - AJ_s(x_2)C(x_2) + \frac{\delta}{\Delta x}[C(x_1) - C(x_2)]$$

Which can be rewritten as:

$$\frac{\partial C}{\partial t}(x,t) + \frac{\partial}{\partial x}\left[-\gamma\frac{\partial P}{\partial x}C(x,t) + \delta\frac{\partial C}{\partial x}\right] = \frac{q(x)}{A}$$

where δ is the diffusion coefficient, and $q(x)$ is the loading and unloading function.

These two conservation equations can be solved to describe the sieve tube flow as it may vary with time. Under certain conditions, however, mathematical instabilities may develop. To date, only transport in short plants has been studied adequately -- either empirically or mathematically. We are using this model to explore the variability that may arise in long distance transport as would be required in trees, and the effects of varying water potential gradients, with both diurnal and seasonal time scales. Tyree *et al.* (1974) found the need of a long slow sink along the path region in order for the Münch Pressure flow theory to account for long distance transport in trees.

The function for loading and unloading of photosynthate ($q(x)$) ultimately links the production by the foliage to the diameter growth of the bole. This crucial linkage will be explored in a time-dependent model in relation to prediction of both growth patterns along the bole and predicted transport rates. These may vary with different tree morphologies and phenologies and these variations will be considered as different species are simulated.

CONSTRUCTION OF A SIMULATOR OF TREE GROWTH

Biological Considerations

The Simple Whole Tree model comprises a series of component models or *kernels*, each of which can be justified as an independent model based on its own theory. We envisage the development of SWT taking place in stages where the overall structure remains as described in Fig. 2 but the precise formulation becomes more integrated, particularly in terms of morphology and the seasonal control of growth patterns. The requirement is to simulate the features that control allocation with increasing effectiveness.

An important challenge in developing SWT will be simulating the vertical pattern of wood increment as a function of differences in sucrose gradient, water potential and a vertical gradient of growth potential. The sink strength of roots will be simulated at various levels to examine the effect this may have, both on root growth itself and upon the growth of the rest of the tree.

SWT constructed at this level will permit an exercise of assessing information on the effects of pollutants on net photosynthetic rates on the growth of trees. SWT will be particularly valuable to make a comparison of the effects of different assumptions about how carbon is distributed to different meristems (i.e., components of the BRANCH model and the distribution functions within the stem) on pollutant influence.

Mathematical and Engineering Considerations

The mathematics underlying much of SWT is expressed as partial differential equations. These result naturally from considerations of flows and diffusion between segments of a compartment and between compartments. They are often of the "reaction-diffusion" type and are relatively complicated. In some cases the underlying finite difference equation is more realistic because the steps of the finite differencing correspond to units of morphology. This is the case, for example, with internodal segments of a branch or the individual cells of a phloem tube. In these cases the partial differential equation is an approximation to the finite difference equation and it may make more sense to simulate the finite difference equation directly. In other cases the partial differential equation is more realistic and it is the finite difference equation that is the approximation. This would be true, for example, for diffusion within a single cell. Thus the partial differential equations that arise in the context of this model are of two types depending on the assumed underlying morphology. The distinction between these two types makes a difference in the

strategy adopted for simulation. In the cases where the morphology is continuous the partial differential equation should be solved with whatever method is most efficient. This may turn out to be using the finite difference equation approximation or not. In the discrete case is usually best to simulate that process directly. However, it may be that solving some variant of the partial differential equation which approximates the finite difference equation is more efficient.

The model is constructed to test hypotheses about both the normal mechanisms of growth of trees and about the impact of pollutants on these mechanisms. Therefore it is important that the model be engineered in such a way as to allow easy modification of these hypotheses. This consideration leads us to adopt the style of programming known as "object oriented" (Meyer, 1988). The necessity of using a modern production language that is highly portable has dictated that we use the C programming language. However, our goal is to write in the style of the C++ language which is an object oriented extension of C (Stroustrup, 1986). When C++ becomes a solid production language available on many operating systems we will switch to that language.

DISCUSSION

Modeling under mechanistic uncertainty

It is worth re-emphasizing that the modeling undertaken here is uncertain both in terms of the details of proposed mechanisms and the functional forms or parametric values used to model them. This reflects the current state of our knowledge about the general mechanisms of tree physiology and growth. It also reflects the fact that any investigation of the effects of pollutants must consider alternative hypothesized mechanisms as does the Forest Response Program. However, this must be carried out in an explicit way.

The role of functional morphology

Finally we wish also to emphasize the role of morphology and phenology in the construction of these models. Morphology provides constraints on the modeling process, the shape of the tree must be predicted as well as the mass. Although this may seem an added burden for the modeler it actually give an added, and very different, way of assessing the effectiveness of a model. The strategy of mixing morphology and physiology into the unified study of "functional morphology" has accounted for many recent successes in animal physiology and we expect that it may do the same for tree physiology.

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CAPTIONS TO FIGURES AND TABLE

Fig.1. Schematic representation of the components in a model for plant growth (Thornley 1972). Growth rate is the result of a dynamic interaction between photosynthesis and nitrogen uptake.

Fig.2. Conceptual model of tree growth processes comprising carbon gain through photosythesis and nutrient uptake. The rates of both these processes and that of water and nutrient uptake and translocation are influence by the morphology of the tree.

Fig.3. Schematic representation of the basic components of BRANCH, a model for branch growth and the export of photosynthate from the branch to the trunk. The model runs for successive annual cycles.

Fig.4. Simulations with BRANCH1

Above : A two dimensional representation of branch morphology, pattern 1 w= 0.7 (see text). Below: Outputs from four simulations that illustrate the differences in shoot extension, export to stem, foliage produced and branch angle, all influenced by differences in branch morphology.

Fig.5. Simulations with BRANCH2

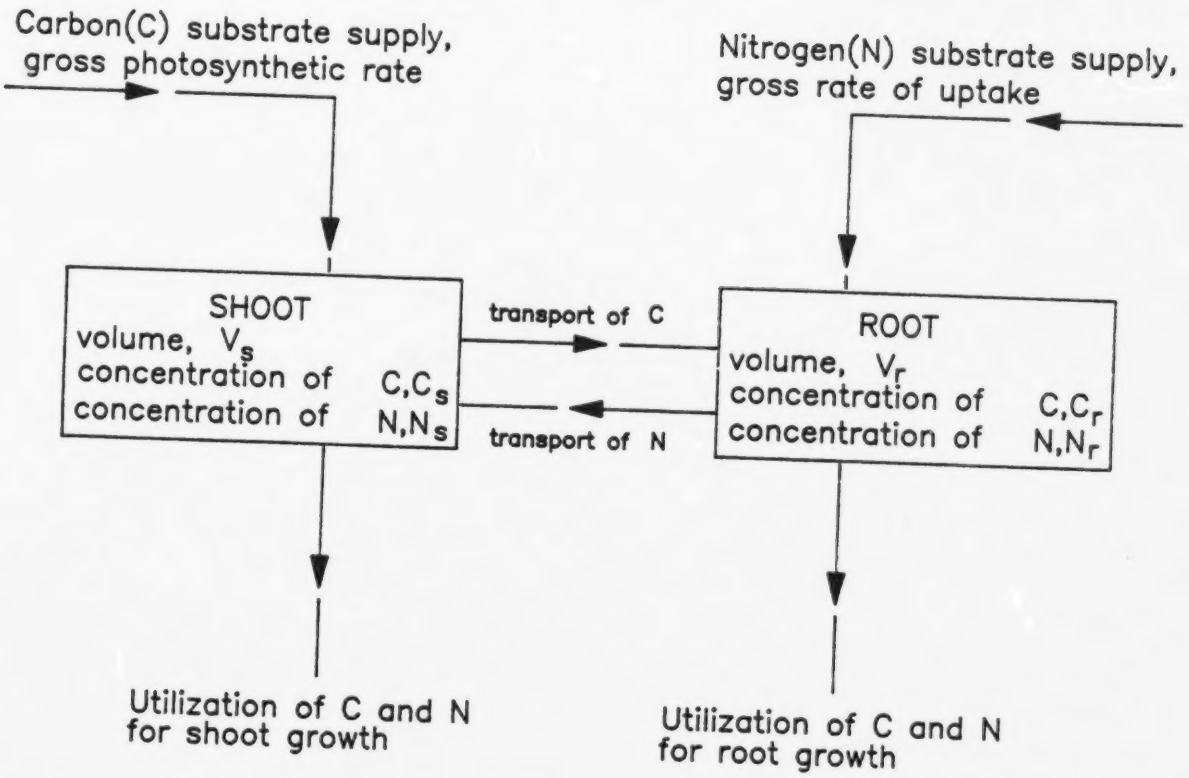
Above : A two dimensional representation of branch morphology, whorlsize 5 (see text). Below: Outputs from four simulations that illustrate the differences in shoot extension, export to stem, foliage produced and branch angle, all influenced by differences in the number of branches in a whorl.

Fig.6. A schematic representation of the flows of water and translocated photosynthate in the region of phloem, cambium and xylem.

Fig.7. A schematic representation of a cylindrical phloem sieve tube showing flows of material and concentration and pressure variables, see Table 1 for named variables.

Table 1. List of Symbols (*after* Smith *et al.*, 1980)

FIG. 1


Carbon(C) substrate supply,
gross photosynthetic rate
Nitrogen(N) substrate supply,
gross rate of uptake
SHOOT
volume, V_s
concentration of C, C_s
concentration of N, N_s
transport of C
transport of N
ROOT
volume, V_r
concentration of C, C_r
concentration of N, N_r
Utilization of C and N
for shoot growth
Utilization of C and N
for root growth

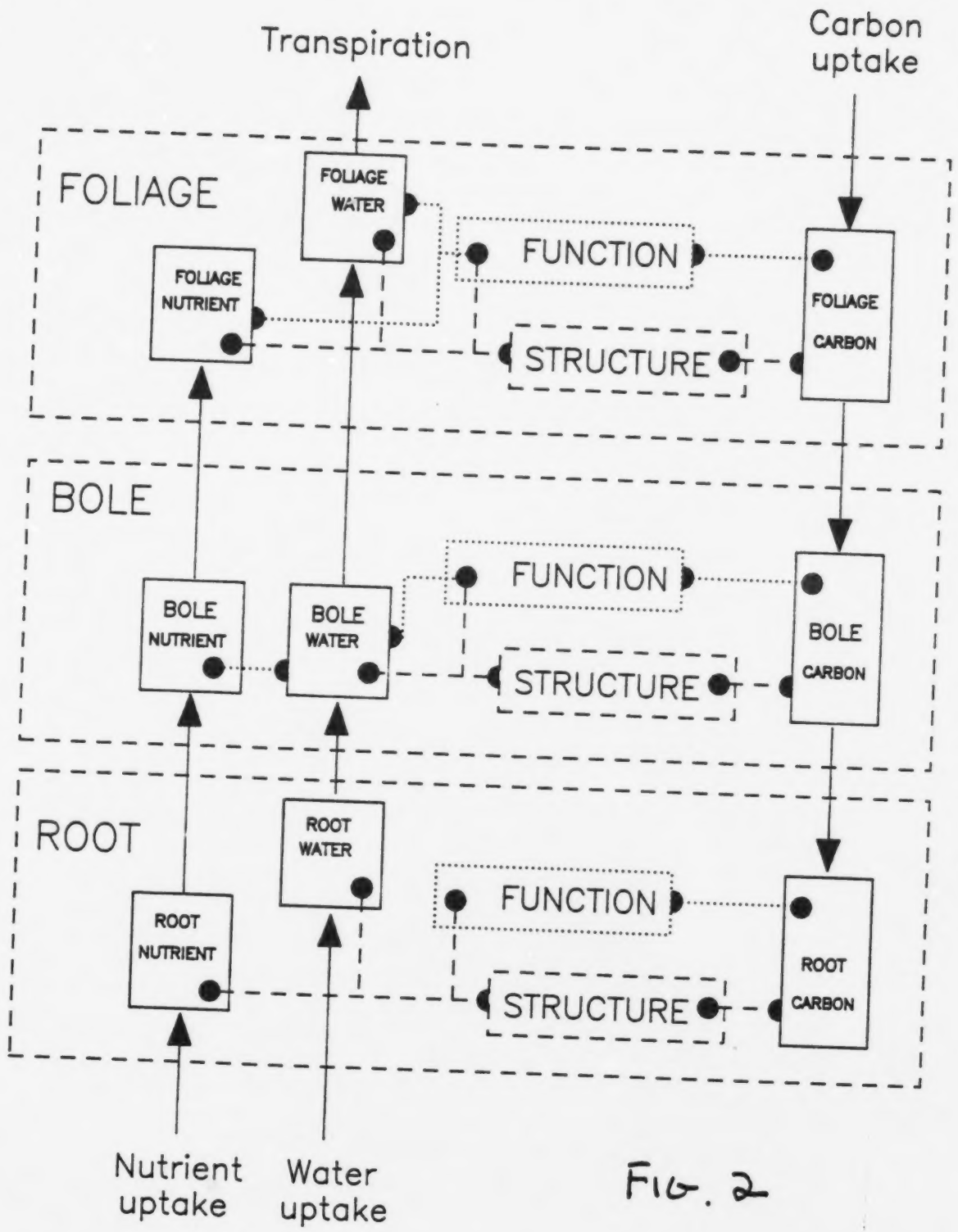

Transpiration
Carbon uptake
FOLIAGE
FOLIAGE WATER
FUNCTION
FOLIAGE NUTRIENT
FOLIAGE CARBON
STRUCTURE
BOLE
FUNCTION
BOLE NUTRIENT
BOLE WATER
BOLE CARBON
STRUCTURE
ROOT
ROOT WATER
FUNCTION
ROOT NUTRIENT
ROOT CARBON
STRUCTURE
Nutrient uptake
Water uptake

FIG. 2

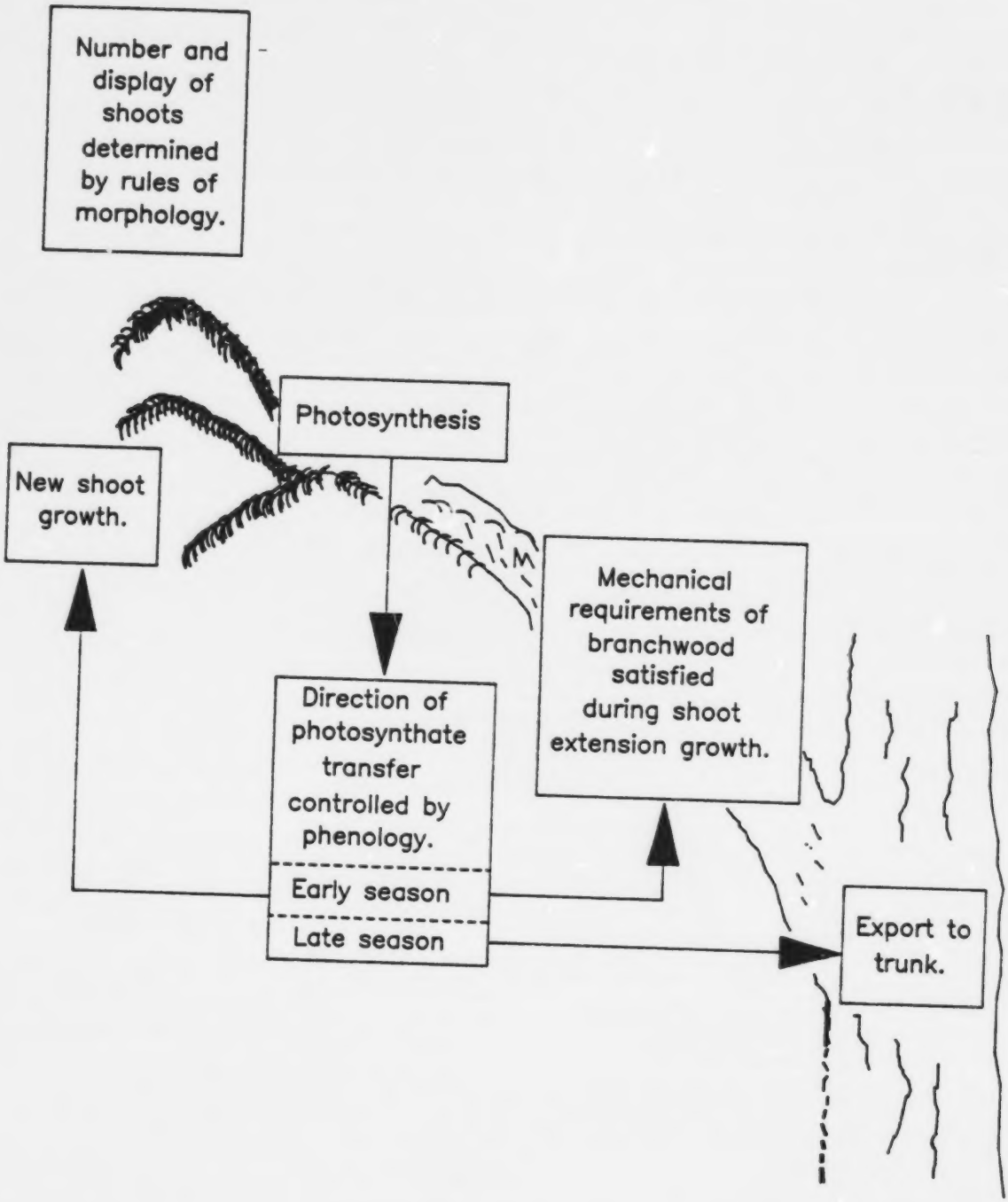

Number and display of shoots determined by rules of morphology.
Photosynthesis
New shoot growth.
Mechanical requirements of branchwood satisfied during shoot extension growth.
Direction of photosynthate transfer controlled by phenology.
Early season
Late season
Export to trunk.

FIG. 3

FIG. 4
TOP

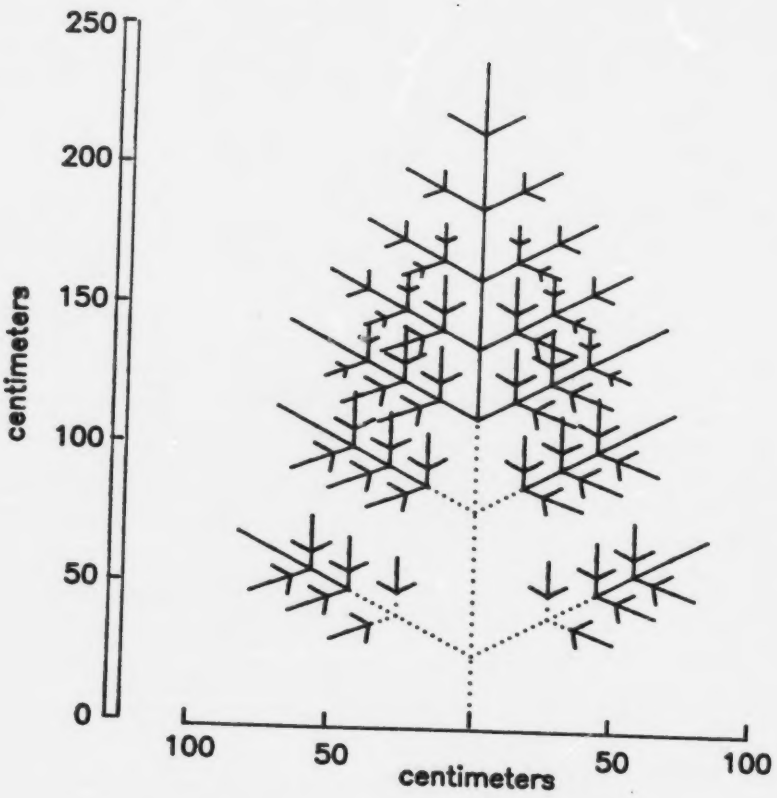
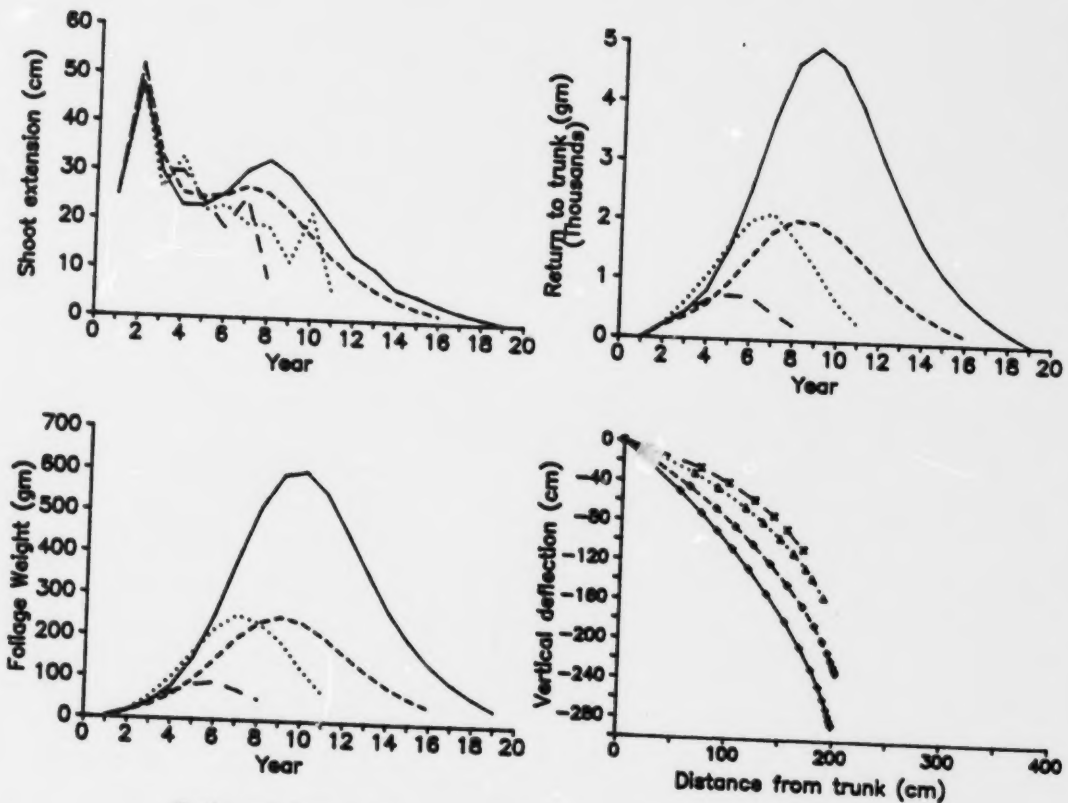


FIG. 4
BOTTOM



Pattern 1; w= 0.7—— , w= 0.5– – .

Pattern 2; w= 0.7···· , w= 0.5—· .

FIG. 5
TOP

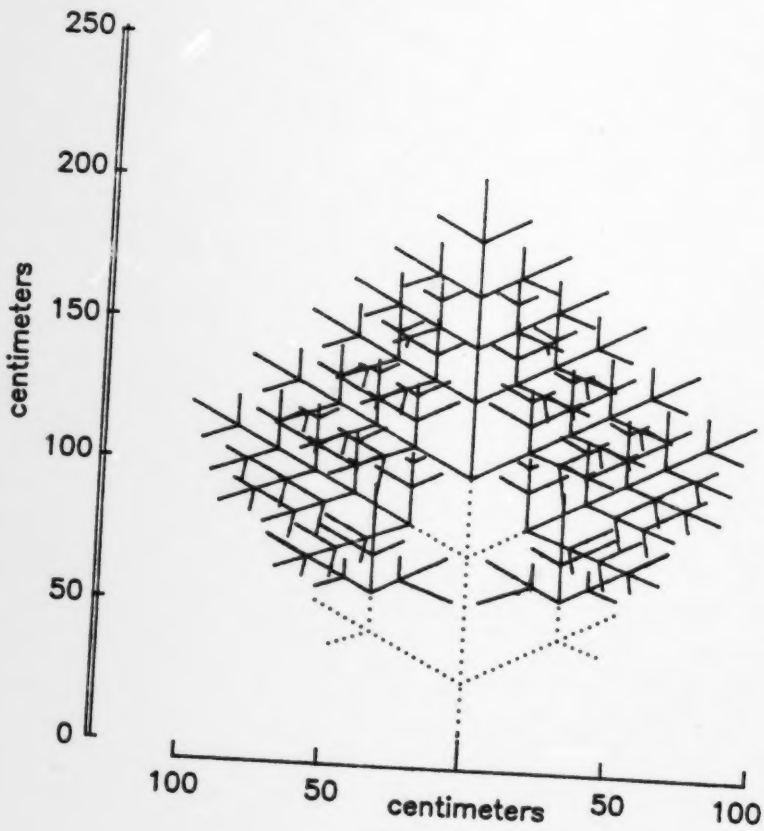


FIG. 5

BOTTOM

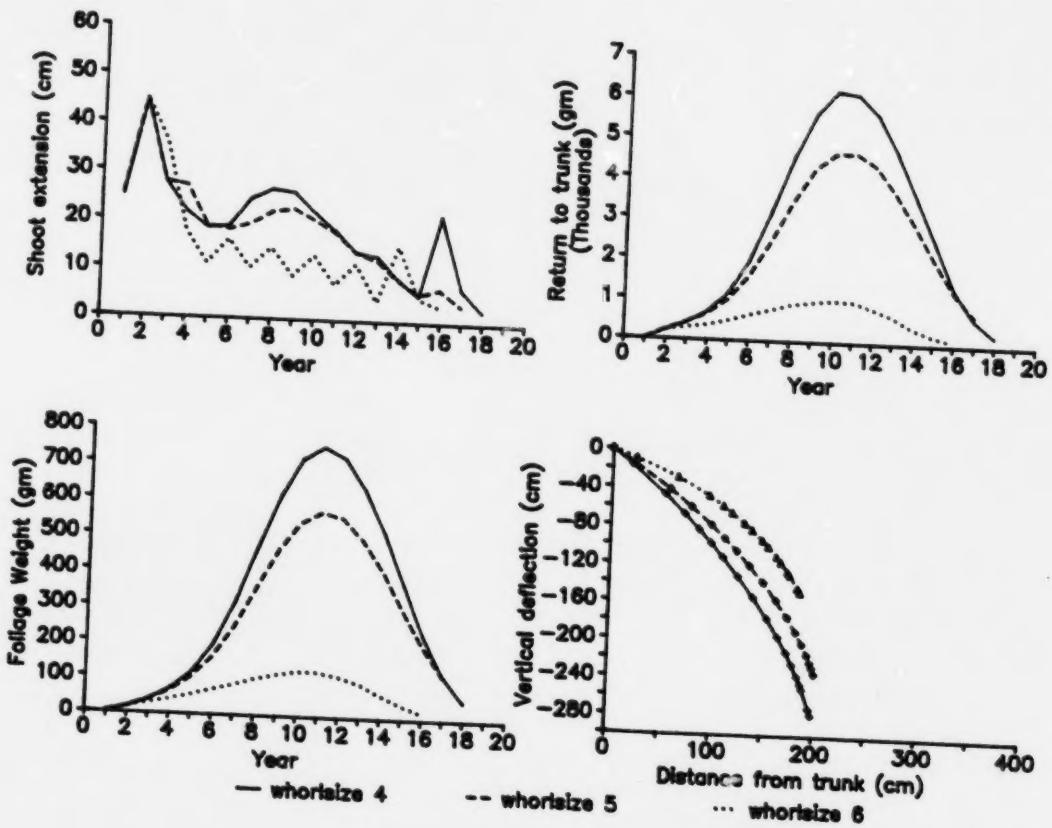
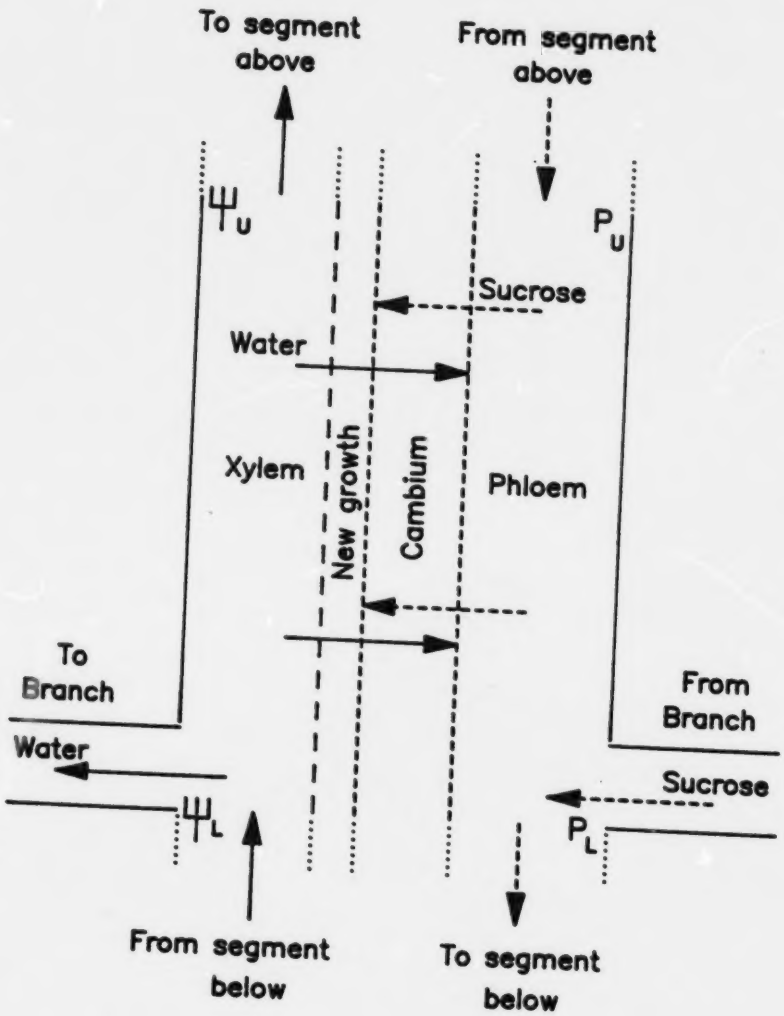

Shoot extension (cm)
Year
Return to trunk (gm) (Thousands)
Year
Foliage Weight (gm)
Year
Vertical deflection (cm)
Distance from trunk (cm)
— whorlsize 4
-- whorlsize 5
··· whorlsize 6

Fig. 6


To segment above
From segment above
Ψ_U
P_U
Sucrose
Water
Xylem
New growth
Cambium
Phloem
To Branch
From Branch
Water
Sucrose
Ψ_L
P_L
From segment below
To segment below

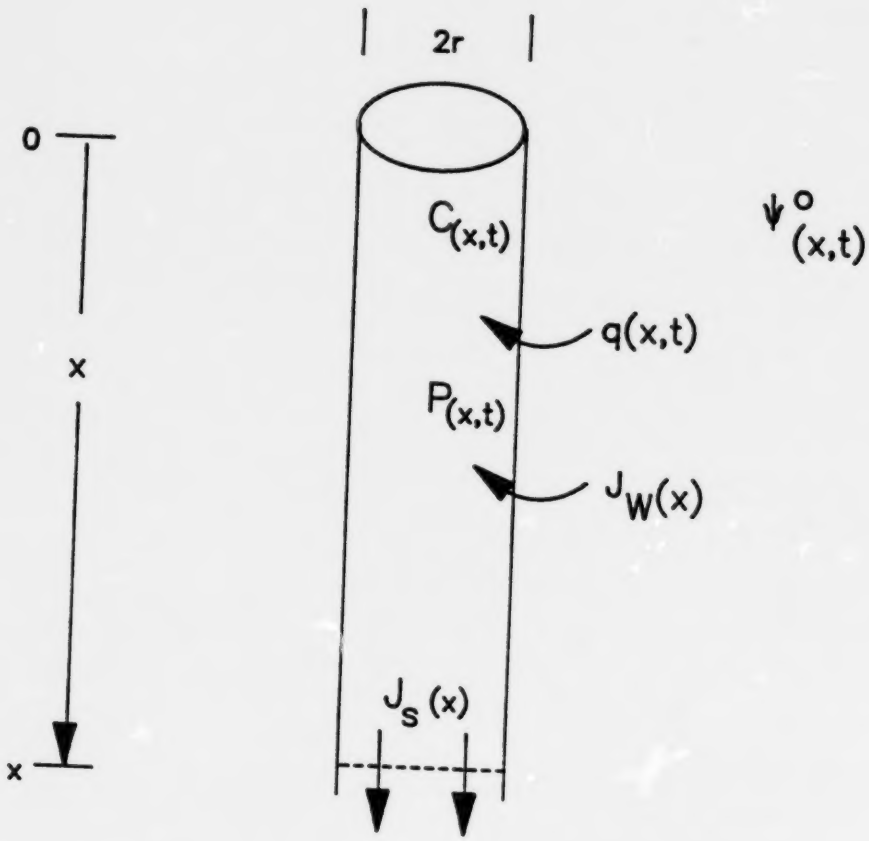


FIG. 7

Table 1. List of Symbols (*after* Smith et al., 1980)

Symbol	Definition	Units
T	Temperature	K
R	Gas Law Constant	cm^3 bar / mol K
$\overline{V}$	Partial molar volume of sucrose	cm^3 / mol
L	Length of sieve tube	cm
$r(x)$	Radius of sieve tube at x	cm
$A(x)$	Cross sectional area at x	cm^2
L_p	Hydraulic conductivity of peripheral membrane at x	cm / bar s
$\gamma(x)$	Conductivity coefficient at x	cm^2 / bar s
$\psi_o(x)$	Water potential of apoplast at x	bars
$\alpha_u(x)$	Unloading coefficient	cm^3 / s cm
$q(x)$	Loading or unloading rate at x	mols / s cm
$J_s(x)$	Velocity of solution at x	cm / s
$J_w(x)$	Volume flux of water through peripheral membrane at x	cm^3 / s cm^2
$P(x)$	Pressure at x	bars
$C(x)$	Concentration at x	mols / cm^3